

Rebuilding beluga stocks in West Greenland

M. P. Heide-Jørgensen^{1,2}, R. G. Hansen^{1,2}, S. Fossette³, N. H. Nielsen^{1,2}, D. L. Borchers⁴, H. Stern⁵ & L. Witting¹

¹ Greenland Institute of Natural Resources, Nuuk, Greenland

² Greenland Institute of Natural Resources, Copenhagen K, Denmark

³ School of Animal Biology, University of Western Australia, Crawley, WA, Australia

⁴ School of Mathematics and Statistics, Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, UK

⁵ Applied Physics Laboratory, University of Washington, Seattle, WA, USA

Keywords

aerial survey; Bayesian assessment; hidden Markov model; line transect; beluga; sea ice cover; abundance estimates; cetaceans.

Correspondence

Mads P. Heide-Jørgensen, Greenland Institute of Natural Resources, c/o Greenland Representation, Strandgade 91,2, DK-1401 Copenhagen K, Denmark.
Email: mhj@ghsdk.dk

Editor: Res Altwegg

Associate Editor: Michael Schaub

Received 22 October 2015; accepted 30 September 2016

doi:10.1111/acv.12315

Abstract

Decisions about sustainable exploitation levels of marine resources are often based on inadequate data, but are nevertheless required for practical purposes. We describe one exception where abundance estimates spanning 30 years and catch data spanning more than 40 years were used in a Bayesian assessment model of belugas *Delphinapterus leucas* off West Greenland. The model was updated with data from a visual aerial survey on the wintering ground in 2012. Methods that take account of stochastic animal availability by using independent estimates of forward and perpendicular sighting distances were used to estimate beluga abundance. A model that appears to be robust to the presence of a few large groups yielded an estimate of 7456 belugas ($cv = 0.44$), similar to a conventional distance-sampling estimate. A mark–recapture distance analysis that corrects for perception and availability bias estimated the abundance to be 9072 whales ($cv = 0.32$). Increasing distance of beluga sightings from shore was correlated with decreasing sea ice cover, suggesting that belugas expand their distribution offshore (i.e. westward in this context) with the reduction of coastal sea ice. A model with high (0.98) adult survival estimated a decline from 18 600 (90% CI: 13 400, 26 000) whales in 1970 to 8000 (90% CI: 5830, 11 200) in 2004. The decline was probably a result of a period with exceptionally large catches. Following the introduction of catch limits in 2004, the model projects an increase to 11 600 (90% CI: 6760, 17 600) individuals in 2020 (assuming annual removals of 294 belugas after 2014). If the annual removal level is fixed at 300 individuals, a low-survival (0.97) model predicts a 75% probability of an increasing population during 2015–2020. Reduced removal rates due to catch limits and the more offshore, less accessible distribution of the whales are believed to be responsible for the initial signs of population recovery.

Introduction

The conservation status of Arctic marine mammals is influenced by hunting levels, habitat changes primarily in the form of sea ice reductions and disturbance by shipping and offshore exploration for development of petroleum resources. As relatively little is known about the actual effects of sea ice loss and disturbance from industrial activities, it seems prudent to at least quantify the effects of hunting. Certainly the impacts of direct removals on any marine mammal population need to be included when assessing the threats from other sources. The only reliable way to monitor trends in population abundance relative to the rate of removals by hunting is through long-term population monitoring. Robust

estimates of absolute abundance exist for only a few Arctic marine mammal populations and long time series that can be used for trend analysis are available for even fewer populations. One example of an Arctic population with both a long and reasonably well-documented history of exploitation and a relatively long time series of abundance estimates spanning three decades is the beluga, or white whale *Delphinapterus leucas*, stock in West Greenland.

Assessment of sustainable exploitation levels for cetaceans subject to substantial exploitation requires frequent estimation of either the absolute size of the hunted population or its relative abundance in the form of an index that reflects changes in abundance. If feasible, absolute abundance estimates are preferred, as they do not rely on assumptions of compatible

survey techniques deployed consistently over decades. Moreover, in the case of a migratory population, it is safer to assess abundance in the area where exploitation occurs rather than having to make assumptions that may be incorrect about the animals' seasonal movements.

Belugas in West Greenland represent such a migratory population, subject to local exploitation in an area experiencing dramatic environmental changes. The belugas arrive in coastal areas of West Greenland in October–November and remain in the area through April. They spend the summer in the Canadian high Arctic around Somerset Island (Innes *et al.*, 2002; Fig. 1). Only one segment of the beluga aggregation near Somerset Island moves to West Greenland in the winter (Heide-Jørgensen *et al.*, 2003). The rest winters in the North Water region in northern Baffin Bay (Heide-Jørgensen *et al.*, 2016) and therefore abundance estimates from Somerset Island (e.g. Innes *et al.*, 2002) are not directly applicable to the population exploited in West Greenland.

Several changes in subsistence hunting in Greenland took place during the 1980s and 1990s. The value of sealskins dropped precipitously due to the collapse of the international

sealskin markets, at the same time that the value of the skin of belugas and narwhals *Monodon monoceros*, the so-called 'mattak', in domestic trade increased dramatically (Heide-Jørgensen, 1994). Introduction of larger fiberglass boats with powerful outboard engines increased both the range and the intensity of hunting effort. As a consequence, restrictions were necessary to prevent further declines in abundance of several marine mammal species under exploitation in Greenland. The beluga was the first of three species, the others being the narwhal and the walrus *Odobenus rosmarus*, to be given some protection from hunting following the advice provided by the North Atlantic Marine Mammal Commission (NAMMCO) and the Canada–Greenland Joint Commission for the Conservation and Management of Narwhal and Beluga. Never before had marine mammals, other than the large whales that fall under the management purview of the International Whaling Commission, been given the benefit of catch restrictions in Greenland and this change was met with anxiety and some resistance in the hunting communities (<http://wwf.panda.org/?20154/The-Big-Four-a-WWF-update-on-Greenlands-efforts-with-regard-to-species-conservation-and-nature-protection>).

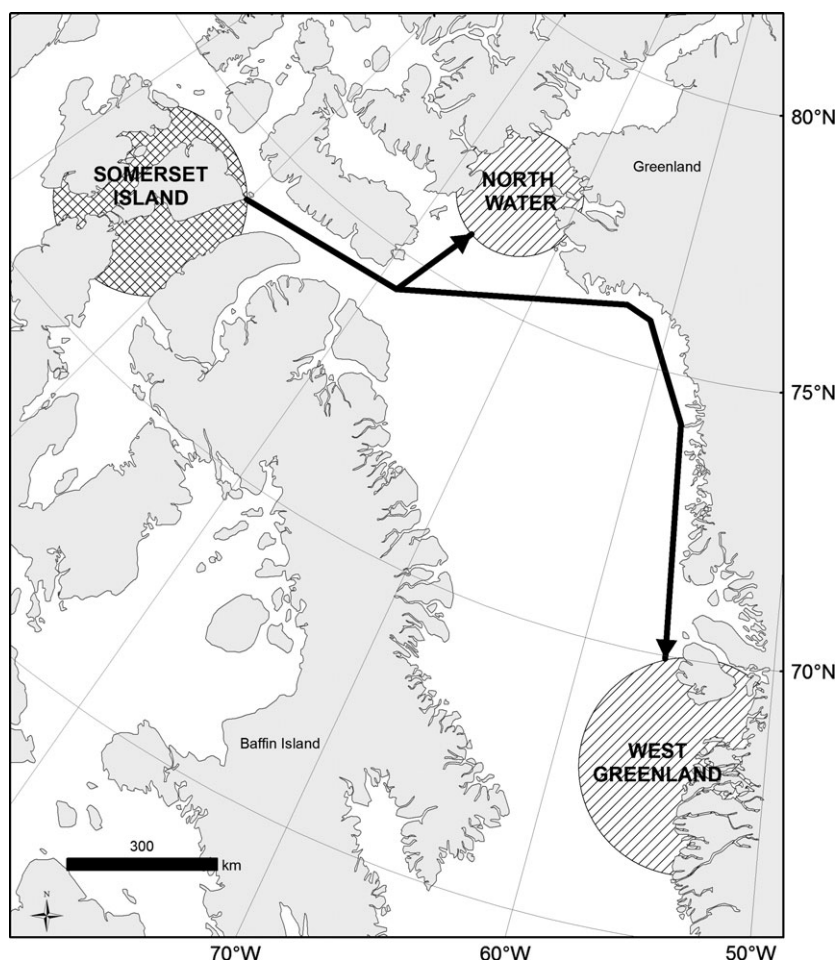


Figure 1 Movements of belugas from summering grounds (double hatched areas) around Somerset Island in North Canada to wintering grounds (hatched area) either in the North Water or along West Greenland south of Disko Island.

The winter occurrence of belugas in West Greenland has been used to obtain an index of trends in the stock hunted from villages along the coast. The area off West Greenland used by belugas during the winter is usually covered with pack ice from January through May. Seasonal sea ice cover in Baffin Bay has essentially confined this wintering population to a fairly well-defined region of about 50 000 km² along the West Greenland coast. The concentration of belugas within this area of mixed open water and loose pack ice facilitates winter surveys of the density and distribution of belugas, nine of which were conducted between 1981 and 2012. The surveys provide both an index and an estimate of the absolute size of the beluga population on the banks off West Greenland (Heide-Jørgensen *et al.*, 2010).

In order to address questions about the effects of habitat change on cetacean populations, it is necessary to have a time series that spans the period of change. The aerial surveys conducted off West Greenland since 1981 provide the only time series of winter habitat use by cetaceans that extends sufficiently far back in time to include the period before sea ice began declining measurably in the Arctic (Xia, Xie & Ke, 2014). Thus, information on the extent of sea ice during a given survey has an important bearing on how survey results are interpreted.

Density estimates of cetacean populations need to be corrected for whales that are not available to be detected at the surface (so-called 'availability bias'). For many species, this correction inflates the abundance estimate substantially because the animals spend a great deal of time underwater and not available to be seen from the aircraft as it passes overhead. Correction factors are often developed by techniques independent of the survey that allow estimation of the proportion of time the whales are expected to be detectable during an over flight. An availability correction factor can be derived from telemetry data of the whales' diving behaviour, but for visual surveys it is assumed that the detection process is instantaneous. This is rarely the case and the longer the animals are within detectable range, the less appropriate such a correction factor will be. Analyses of previous aerial surveys of belugas in West Greenland assumed that the search effort was nearly instantaneous. To test this assumption we applied a density estimation method [*hidden Markov line transect model (hmltm)*; Borchers *et al.*, 2013] that takes into account both the forward distance of detections and the stochastic sequence of durations of surfacing and diving by belugas.

The beluga population in West Greenland has undergone some drastic changes, attributed in large part to the effects of hunting (Alvarez-Flores & Heide-Jørgensen, 2004). Controlling the rate of removals by hunting is crucial to conservation and this study provides a new assessment to establish sustainable levels of exploitation of belugas in West Greenland. This assessment is based on new estimates of total abundance combined with a Bayesian age- and sex-structured population dynamics model with density-regulated growth. The model is initiated with a stable age structure in 1970 and projected under the assumption that the abundance in

1970 was below the carrying capacity at that time. Changes in beluga distribution and exploitation in relation to changes in sea ice cover during the past 35 years are examined as well.

Materials and methods

Field techniques

A visual double-observer aerial line transect survey was conducted using a fixed-winged aircraft (Twin Otter, De Havilland, Toronto, Canada) equipped with four bubble windows flying at a target altitude and speed of 213 m and 166 km h⁻¹ respectively. The front (observer 1) and rear (observer 2) observers acted independently of each other, recording declination angles to sightings (using an inclinometer, Suunto, Vantaa, Finland) as well as species and group size when the animals passed abeam. Time in view was recorded as the difference between the time at first sighting and time when the sighting passed abeam. Beaufort sea state and glare were recorded at the start of the day and whenever they changed. Decisions about duplicate sightings (animals seen by both observer 1 and 2) were based on coincidence in timing and positions, group size and direction of movement. Declination angles (ω) measured when animals were abeam were converted to perpendicular distances (x) using the following equation from Buckland *et al.* (2001): $x = v \times \tan(90 - \omega)$, where v is the altitude of the airplane. Forward distance (y) to each sighting was calculated based on time of first sighting, time when passing abeam and speed of aircraft.

The survey was conducted from 24 March to 15 April 2012 covering the area between 65°40'N and 75°30'N (Fig. 2; Table 1) and observers recorded sightings of all marine mammals. Sixteen strata with 116 transect lines were identified and these lines were systematically placed so that east-west density gradients would be crossed.

Analysis of sea ice conditions at each sighting

Still images of the area (150 × 100 m) directly under the aircraft, with a 10% overlap, were continuously captured by a Nikon D300S camera using a 50-mm fixed focal length lens (Nikon Corporation, Tokyo, Japan). To use as a potential factor in the detection function analysis, ice coverage was assigned to one of four categories. Least-affected sighting conditions were classified as category 1 and most-affected as category 4. Category 1 included close to 100% ice coverage at the locality of the sighting (only leads of open water), category 2 included 100% ice coverage (no leads), category 3 included a complex mosaic of broken ice (value between 30 and 99% ice coverage), category 4 included a complex mosaic with between 1 and 30% ice coverage. Detection under the four ice coverage categories is shown in Supporting Information (Fig. S9).

To allow for comparison with previous surveys, and in the absence of data specific to the time and area of the survey, an

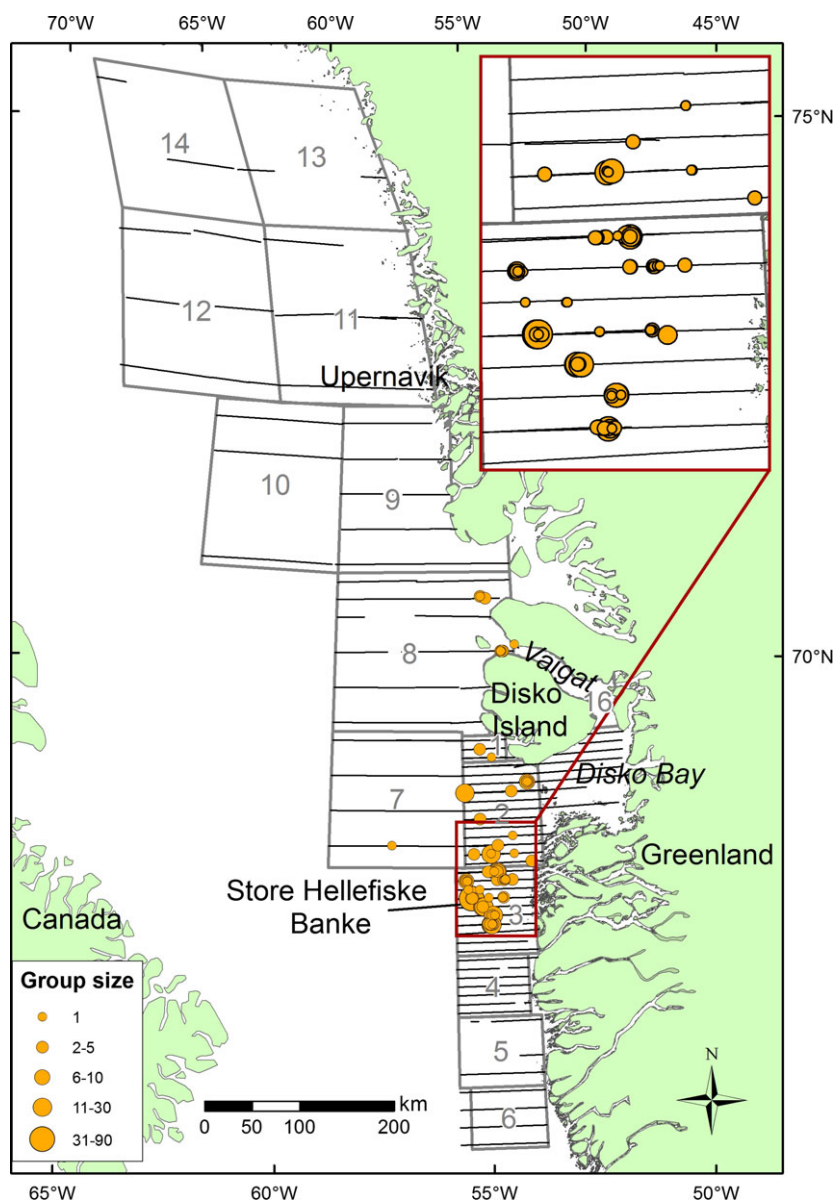


Figure 2 Stratification realized transect lines in sea state ≤ 2 and observations of belugas in West Greenland during aerial surveys in March–April 2012.

estimated mean proportion of time available for detection of 43% ($cv = 0.09$, see Heide-Jørgensen *et al.*, 2010) was used to correct both the conventional and mark–recapture distance sampling (*mrd*s) estimator of abundance for availability bias.

Density estimation using the *hmltm*

A modification of the *hmltm* of Borchers *et al.* (2013) and Rekdal *et al.* (2015) was used to estimate the detection probability, density and abundance of belugas. This involved first estimating the parameters of a hidden Markov model for whale availability and then integrating these with the line transect data, using both perpendicular and forward distances,

to detected whales to estimate detection probability (see Borchers *et al.*, 2013 for details).

No data exist on the dive cycle of belugas on their wintering ground in West Greenland and logistical difficulties prevent such data from being collected with currently available techniques. Instead dive cycle observations from Martin & Smith (1999) were incorporated into a two-state Markov model for the time series of states (see Supporting Information), and Bernoulli random variables with the parameters $Pr(avail|state\ 1)$ and $Pr(avail|state\ 2)$ for availability were used given the hidden states.

Estimation methods for detection function parameters, group size, group abundance and animal abundance are

Table 1 Stratum area, number of transects (*k*), search effort (*L*), beluga sightings (*n*) and sighting rate (*n/L*) for the 16 strata surveyed in March–April 2012

Stratum	Area (km ²)	<i>k</i>	Effort (<i>L</i>) (km)	<i>n</i>	<i>n/L</i>	cv (<i>n/L</i>)
1	1275	3	191.0	1	0.0052	0.74
2	8941	12	1382.6	17	0.0123	0.43
3	7813	10	977.6	38	0.0389	0.27
4	4928	7	521.1	0		
5	6605	3	173.5	0		
6	5180	4	504.8	0		
7	20 194	4	633.5	1	0.0016	0.90
8	28 677	6	942.7	6	0.0064	0.92
9	22 461	5	618.7	0		
10	24 522	2	267.7	0		
11	29 437	3	408.1	0		
12	29 466	3	467.0	0		
13	21 475	1	25.7	0		
14	21 501	2	139.9	0		
15	7142	9	576.1	0		
16	3036	1	6.7	0		
Total	242 650	75	7836.5	63	0.0080	0.23

Strip width is truncated at 100–900 m and cv is the coefficient of variation.

described in Supporting Information. Model selection was based on Akaike Information Criteria (AIC) and goodness-of-fit *P*-values for all models that converged. Coefficients of variation (cv's) were obtained by bootstrapping mean durations of dive cycle and time available from the Markov model for availability, and bootstrapping transects within strata. A total of 1000 bootstrap resamples were drawn and confidence intervals were obtained from the point estimate and cv assuming log normality.

Density estimation using conventional and *mrds* models

Both a *conventional distance sampling* (*cds*, Buckland *et al.*, 2001) and a *mrds* analysis that accounts for the so-called 'perception bias' for animals available at distance 0 but missed by the observers (Laake & Borchers, 2004) were applied to the survey data. Encounter rate and cluster size were estimated by stratum, with detection probability pooled across all strata. Variances and confidence intervals were estimated as above.

Information on sea ice conditions

Data on sea ice conditions in Baffin Bay were obtained from monthly gridded sea ice concentration products derived from satellite passive microwave data using the NASA Team algorithm (Cavalieri *et al.*, 1996, updated yearly), available from the National Snow and Ice Data Center in Boulder, Colorado, USA. Sea ice concentration is the fraction of ocean area covered by sea ice. Each sea ice concentration grid is mapped to a polar stereographic projection (true at 70°N) with a nominal grid cell size of 25 × 25 km. The 'medium area' (boundaries: 65–70°N, and from the west coast of

Greenland to 58°W; 193 grid cells; 118 600 km²) along West Greenland defined in Stern & Heide-Jørgensen (2003) was used for estimation of the annual sea ice area in the beluga habitat off West Greenland. The sea ice concentration in March, typically the month with the highest concentration, was used to compute an area-weighted average over all grid cells to estimate the mean winter sea ice area. Thus, the monthly estimates of sea ice area involved spatial and temporal averaging.

Population dynamics model

A Bayesian population dynamics model was fitted to relative and absolute indices of winter abundance of belugas off West Greenland. We used an age- and sex-structured population dynamics model (see Supporting Information) with an even sex ratio and a Pella–Tomlinson form of density regulation on the birth rate (Pella & Tomlinson, 1969). Fecundity was assumed to be identical for all mature females, with yearly survival (*p*) being constant across all age classes, except for the first year of life where calf survival (*p_{0p}*) was determined as a fraction (*p₀*) of adult survival (*p*).

The shape parameter (*γ*) of the density regulation function was set to values between two and four to obtain a maximum sustainable yield (*msy*) around a *msy* level (*msyl*) of 60% of the carrying capacity (*N**). The growth potential of the population was estimated by the *msy* rate (*msyr*).

Catches were assumed to be taken evenly from females and males as the sexes of animals in the catches were not reported, and they were taken in proportion to the age structure in the population, except that no calves (<1 year) were assumed to be taken. Two catch histories (Supporting Information Table S1) were used in the population dynamics modelling to reflect uncertainty in the number of animals removed. A low catch history was corrected for under-reporting and a high catch history was corrected for both under-reporting and killed-but-lost whales. Both options included mortality associated with ice entrapment events. Removals in Canada (during the summer) from the population exploited in West Greenland (during the winter and spring) are considered to be so low that they would not have affected the population dynamics significantly (Innes & Stewart, 2002).

The population model was fitted to the relative and absolute indices of winter abundance off West Greenland (Supporting Information Table S2) by Bayesian integration (Supporting Information). This integration was based on the sampling–importance–resampling routine (Jeffreys, 1961; Berger, 1985; Rubin, 1988), and it used log-normally distributed observation errors and an additional variance term to estimate posterior parameter distributions from priors.

Prior distributions

All the priors were uninformative and uniform covering ranges that reflect likely parameter values for beluga (Table 2), with the *dB* model representing high adult survival (0.97–0.995) and the *dB_l* model representing low adult survival (0.945–0.995).

The prior on the maximum birth rate was symmetrical around a value of 0.33 that corresponds with an average birth interval of 3 years. This was in the lower range of a typical 2- to 3-year birth cycle in beluga and narwhal (Braham, 1984; Garde *et al.*, 2015), and it agrees with a sample of belugas from West Greenland where 11 out of 36 mature females were pregnant (Heide-Jørgensen & Teilmann, 1994). Our upper prior value of 0.4 was just below a reported pregnancy rate of 0.41 for beluga in the eastern Chukchi Sea (Suydam, 2009). Ideally this should be applied as a prior on the birth rate at the time of sampling, but this is not straightforward, and it was applied here as a prior on the maximum birth rate. Our birth rate prior was therefore most likely conservative and negatively biased.

A uniform prior between 6 and 12 was set on the age of the first reproductive event. It was based on an estimate of 8.3 for female beluga (Suydam, 2009) and an estimate of 8.5 for the age of maturity in female narwhal (Garde *et al.*, 2015). This indicates an average value around 9 years of age, with the 6- to 12-interval including a high point estimate of 11.8 for female narwhal (Hay, 1980).

A uniform prior between zero and one was set as a scaling (c_h) of the catch history, with the low catch history being subtracted from the dynamics for $c_h = 0$, the high catch history being subtracted for $c_h = 1$ and a linear combination in between.

The priors on abundance assume that the population was below the carrying capacity in 1970. For a given draw of the carrying capacity (N^*), this is ensured by drawing the 1970 abundance (N_0) from a uniform prior $U(5K, N^*)$.

Results

Distribution of sightings

In 2012, a total of 7800 km was flown over 75 transects in 16 strata covering a total area of 242 650 km² (Table 1). Belugas were observed in 5 out of 16 strata and they were found primarily in coastal areas along West Greenland and in shallow water (<200 m deep, Fig. 2). No belugas were observed south of 67.7°N or north of 71°N and none were detected in Disko Bay. Belugas were seen in the highest densities at the northern edge of Store Hellefiske Bank, southwest of Disko Bay. They were also found in the northern opening of Vaigat and off Uummannaq.

When including the previous nine surveys of belugas in West Greenland, a significant correlation was detected

between the longitude of sightings (i.e. distance from the coast) and the extent of sea ice, that is, the more pack ice in Baffin Bay, the closer to the coast belugas were observed at the time of the survey (ANOVA, $P = 0.002$, Fig. 3). However, this correlation is strongly driven by the observations in 2006 when little sea ice was present. If 2006 is excluded from the analysis, the trend can still be seen but it is no longer significant ($P = 0.08$).

Density estimation using the *hmltm*

The 2012 survey generated 89 detections of beluga groups with perpendicular distances, of which 59 also had forward distance at the time of sighting. Exploratory analyses led to left truncation of perpendicular distances at 100 m and right truncation at 900 m (Supporting Information Fig. S10). This reduced the number of detections to 63, and the number with forward distance estimates to 44.

The *ice* covariate was discarded because models without *ice* were selected above models that included *ice* (see Supporting Information).

Estimates of total abundance, mean probability of detection at perpendicular distance zero and mean group size are shown in Supporting Information (Tables S4–S6). Three models with AIC differences of less than two gave density estimates with 95% confidence intervals of 8684 (2073, 37 045), 7549 (2209, 26 378) and 7456 (3293, 16 987).

There is good agreement among the three models in the estimates of group abundance (N.grp in Supporting Information Tables S4–S6) and the associated cv's, but not in the estimates of individual abundance and cv's. In particular, the individual abundance cv's for the two models with more parameters and lower AICs (belEP2x.bfy and belEP2x.waitx) are roughly twice as large as the group abundance cv's, while for model belEP2x.null, the individual abundance cv is almost the same as the group abundance cv. The main driver of the change in cv's is the mean group size estimate in the stratum with highest abundance (Stratum 3) and highest mean group size (this is the stratum with an observed group size of 90 – three times larger than any other observed group size). The less flexible belEP2x.null model is more robust to this large group size variation and therefore the estimate 7456 belugas (95% CI: 3293–16 987) from this model is considered to be most reliable.

Two alternative models for availability (models 2 and 3 – see Supporting Information Tables S8 and S9) resulted in changes in estimated abundance of only about 2%, so

Table 2 Prior distributions for the different models (*M*)

<i>M</i>	N_0	N^*	p	p_0	b_{\max}	a_m	γ	c_h	β_a	β_b	σ_b
<i>dB</i>	$U(5, N^*)$	$U(10, 50)$	$u(0.97, 1)$	$u(0.5, 1)$	$u(0.26, 0.40)$	$u(6, 12)$	$u(2, 4)$	$u(0, 1)$	$U(0.05, 0.5)$	$U(0.05, 0.2)$	$u(0, 0.5)$
<i>dB1</i>	$U(5, N^*)$	$U(10, 50)$	$u(0.95, 1)$	$u(0.5, 1)$	$u(0.26, 0.40)$	$u(6, 12)$	$u(2, 4)$	$u(0, 1)$	$U(0.05, 0.5)$	$U(0.05, 0.2)$	$u(0, 0.5)$

The female fraction at birth (θ) is assumed to be 0.5. The prior probability distribution is either uniform, $u(\min, \max)$, or log uniform, $U(\min, \max)$.

List of parameters: N_0 , initial abundance; N^* , population dynamic equilibrium abundance in thousands; p , yearly survival; p_0 , first-year survival; b_{\max} , maximal birth rate; a_m , age of the first reproductive event; γ , density-dependent regulation; c_h , catch history; β_i , abundance estimate bias (*i*: data reference); σ_i , additional variance (*i*: data reference).

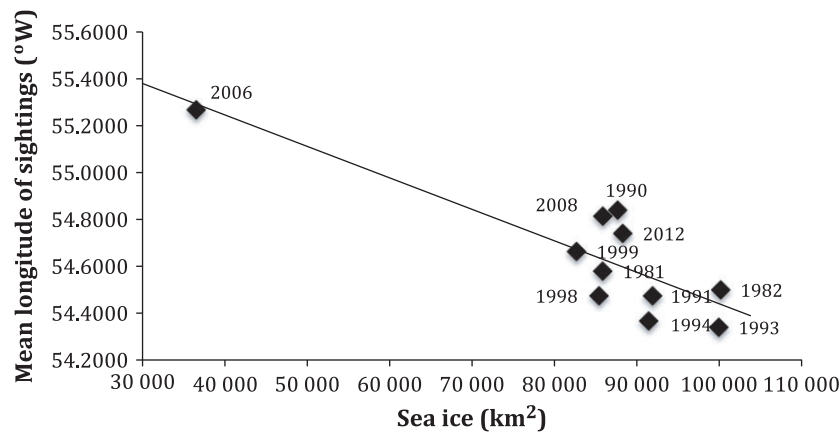


Figure 3 The correlation between sea ice extent ('medium area' of West Greenland in Stern & Heide-Jørgensen, 2003) and the average longitude of beluga sightings (between 67 and 70°N and east of 56°W) during mid-winter surveys between 1981 and 2012. The correlation between longitude of sightings and sea ice area is significant (ANOVA, $P = 0.002$), unless 2006 is excluded.

although the dive cycle length of belugas wintering in West Greenland is not well known, the abundance estimate is quite insensitive to a range of plausible dive cycle lengths.

Density estimation using conventional and *mrds* models

The half-normal detection function model used observations from both observer 1 and 2 and was chosen for *cds* on the basis of AIC (Supporting Information Fig. S11). The associated Cramer–von Mises goodness-of-fit statistic had a P -value > 0.9 and the *cds* analysis yielded an abundance estimate of 7546 whales ($cv = 0.38$, 95% CI: 3461, 16 450).

The half-normal detection function model with no variables was chosen for the *mrds* on the basis of AIC (Table 3; Fig. 4) and yielded an abundance estimate of 9072 whales ($cv = 0.32$, 95% CI: 4895, 16 815) with a $g(0) = 0.94$ for both observers. Both the conventional and the *mrds* estimates were corrected for availability bias.

Population dynamics

Plots of the realized prior and posterior distributions are shown in Supporting Information (Figs S12 and S13) for the models with high (*dB*) and low (*dB*) adult survival. Both models behave almost similar with a clear updating of the abundance-related priors (N_0 , N^* , β , σ) and almost no updating of the life history (p , p_0 , b_{max} , a_m) and growth rate-related parameters ($msyr$, $msyl$). Yet, the *dB* model shows some updating towards higher survival rates and population growth than assumed by the prior.

The posterior parameter estimates showed good agreement between all parameters with almost no difference in the estimated *msyr* of the two models (Table 4). Both models estimate a population trajectory that shows a continuous decline from 1970 through 2003, the year when catch limits were first implemented, and a slight increase after 2004 with a projected continued increase through 2020 (Fig. 5). The high

Table 3 Mark-recapture distance sampling model showing AIC values after fitting explanatory variables to the DS and MR models

Model	DS model	MR model	AIC	dAIC
1	<i>d</i>	<i>d</i>	937.27	0.00
2	<i>d + gs₄</i>	<i>d</i>	938.94	1.67
3	<i>d</i>	<i>d + o</i>	938.41	1.14
4	<i>d + bf</i>	<i>d</i>	938.71	1.44
5	<i>d</i>	<i>d + gs₄</i>	937.79	0.52
6	<i>d</i>	<i>d + bf</i>	938.81	1.54
7	<i>d</i>	<i>d + bf + gs₄</i>	938.81	1.54

The chosen model is given in bold and 'dAIC' indicates the difference between the chosen model and the specified model. The half-normal form for the DS model was chosen based on lowest AIC. The explanatory variables are perpendicular distance (*d*), Beaufort sea state (*bf*), group size as a factor with four classes (1, 2–4, 5–10, 12–90) (*gs₄*) and observer (*o*).

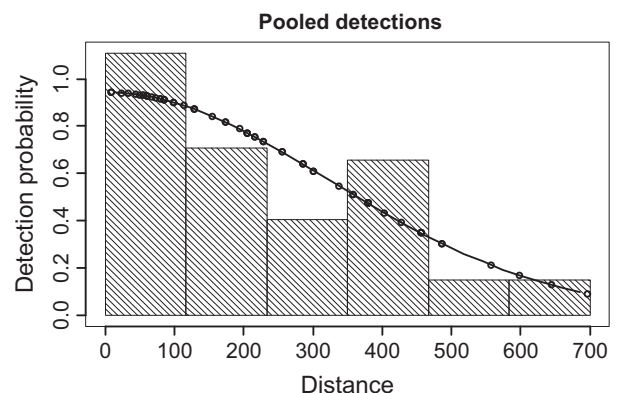


Figure 4 Half-normal detection function fit to perpendicular distance data from mark-recapture distance sampling analysis.

survival (0.98) model (top panel) estimates a decline from 18 600 (90% CI: 13 400, 26 000) whales in 1970 to 8000 (90% CI: 5830, 11 200) in 2004, and it projects an increase

to 11 600 (90% CI: 6760, 17 600) individuals in 2020 (assuming annual removals after 2014 of 294 belugas).

The trade-off space between future catches from 2015 to 2020 and the probability of an increasing population are shown in Fig. 6, for yearly catches between 200 and 400. Given total annual removals of 300 individuals from 2015 to 2020, the low survival (0.97) model estimates that there will be a 75% chance of an increasing population over this period, and the high survival (0.98) model estimates 87% chance of increase.

Discussion

Density estimation

Although animals are detected as far as 925 m ahead of the aircraft, at a flying ground speed of 160 km h⁻¹ this corresponds to their being within detectable forward range for only about 1.7% (0.925/160*60/20.47) of their mean dive cycle length. From this perspective, the survey is nearly instantaneous. Therefore, methods that correct *cds* estimates by dividing either the proportion of time animals are available on average (0.43 with our availability model) or the probability of animals becoming available at least once while within detectable forward distance (about 0.46 with our availability model, using the method of Laake *et al.*, 1997 and maximum forward distance of 1000 m) should be nearly unbiased. We estimate from our *hmltm* analysis using forward detection distance that the probability of detecting an animal at perpendicular distance zero is 0.44 (see Supporting Information Table S3). This is similar to both of these correction factors, and between the two values – as would be expected.

The *hmltm* has the advantage that it uses the forward distances to estimate detection probability, whereas *cds* methods rely only on perpendicular distances. However, the use of these data comes at the cost of having to model detection probability in two dimensions rather than one. When the survey is far from instantaneous, this cost can be heavily outweighed by the reduction in bias that comes from using the forward distances. When the survey is close to instantaneous,

as here, the benefits of using the forward distances are not as great.

With these data, the best *hmltm* yields an abundance estimate that is within 1% of that from a *cds* analysis corrected for availability bias by dividing by the estimated mean proportion of time animals are available for detection. Because it does not involve estimation of parameters related to forward distance distribution, the *cds* estimator has a lower cv (38% compared to 44% for the *hmltm*). Given that the time animals are in view is only about 1.7% of their dive cycle length, the survey must be considered nearly ‘instantaneous’. So use of an ‘instantaneous’ survey availability correction factor of 0.43 should lead to little, if any, bias (a conclusion supported by the fact that the estimate of $p(0) = 0.44$ from the *hmltm* is close to the availability correction factor of 0.43). When estimating density using *hmltm*, perception bias is not accounted for, and considering that the survey is nearly instantaneous, the density estimated from the *mrds* model, which corrects for perception bias, is thought to be the most reliable, with an abundance estimate of 9072 whales (cv = 32%).

Trends in abundance

There is little doubt that the decline in abundance of belugas in West Greenland from 1970 to 2003 was caused by excessive hunting pressure, as also documented in previous assessments (Butterworth, Plagaányi & Geromont, 2002; Innes & Stewart, 2002; Alvarez-Flores & Heide-Jørgensen, 2004).

The abundance estimate of 9072 belugas (cv = 32%) in 2012 from the *mrds* represents a slight decrease in abundance compared to the last abundance estimate of 10 595 (cv = 43%) belugas in 2006 (see Fig. 5; Heide-Jørgensen *et al.*, 2010), but is larger than an estimate from 1999 of 7941 belugas (95% CI: 3650, 17 278) (Heide-Jørgensen & Acquarone, 2002). None of the estimates are significantly different. Several scenarios may explain the recent (after 2004) fluctuations in abundance of belugas in West Greenland. The continued hunting causes direct mortality, which of course affects the abundance and density of belugas in

Table 4 Parameter estimates for the different models (*M*)

<i>M</i>		N_0	N^*	p	p_0	b_{\max}	a_m	γ	c_h	β_a	β_b	σ_b	$msyr$	$msyl$
<i>dB</i>	$x_{0.5}$	19	28	0.98	0.77	0.33	9	3.0	0.39	0.18	0.09	0.12	0.03	0.67
	$x_{0.05}$	13	19	0.97	0.54	0.27	6.3	2.1	0.03	0.12	0.07	0.01	0.02	0.62
	$x_{0.95}$	26	47	0.99	0.98	0.39	12	3.9	0.92	0.25	0.14	0.38	0.05	0.71
<i>dbI</i>	$x_{0.5}$	20	30	0.98	0.78	0.34	9	3.0	0.40	0.17	0.09	0.13	0.03	0.67
	$x_{0.05}$	14	19	0.95	0.54	0.27	6.3	2.1	0.03	0.11	0.06	0.01	0.01	0.62
	$x_{0.95}$	30	47	0.99	0.98	0.39	12	3.9	0.93	0.24	0.13	0.38	0.05	0.70

Estimates are given by the median ($x_{0.5}$) and the 90% credibility interval ($x_{0.05} - x_{0.95}$) of the posterior distributions.

List of parameters: N_0 , initial abundance (in thousands); N^* , population dynamic equilibrium abundance (in thousands); p , yearly survival; p_0 , first-year survival; b_{\max} , maximal birth rate; a_m , age of the first reproductive event; γ , density-dependence parameter; c_h , catch history; β_i , abundance estimate bias (*i*: data reference); σ_i , additional variance (*i*: data reference), $msyr$, maximum sustainable yield rate; $msyl$, msy level.

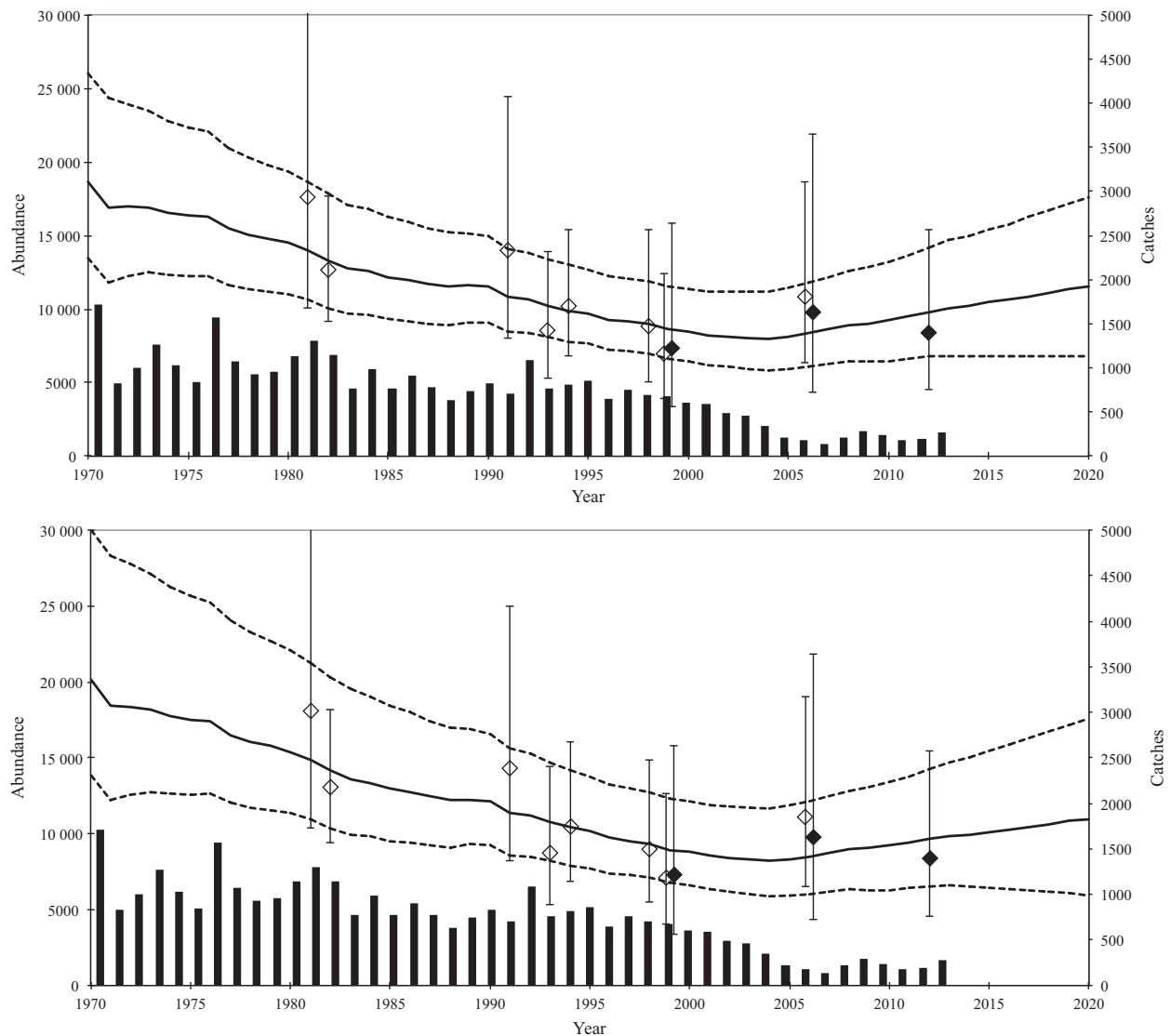


Figure 5 The projected median and 90% credibility interval together with the absolute abundance estimates (solid diamonds) and the rescaled relative estimates (open diamonds). Top plot, *dB* model; bottom plot, *dBI* model. Catches shown as histograms below.

West Greenland. Accessibility of the whales to the hunters is affected by the extent of sea ice. A large extent of sea ice forces the whales closer to the coast and within reach of the hunting communities (Fig. 7; Heide-Jørgensen *et al.*, 2010). The stock of belugas that winters in West Greenland is part of the larger aggregation that is found in the summer in inlets and bays along Somerset Island in northern Canada. Only a portion of the whales from Somerset Island move to West Greenland for the winter, while the other portion winters in the North Water area in northern Baffin Bay (Heide-Jørgensen *et al.*, 2003). It is unknown if the apportioning of whales between the two wintering areas fluctuates from year to year. It is also possible that undiscovered ice entrapments cause mortality or that excessive disturbance from fishing

activities or seismic survey activity reduces the fraction of the Somerset Island belugas that ends up wintering off West Greenland in a given year (cf. Heide-Jørgensen *et al.*, 2012).

Population dynamics

The upper tail of the posterior on the maximum birth rate have 95 percentiles of 0.39 for both models (Table 4). These estimates match the 5th percentile estimate of 0.54 for p_0 , where the maximum birth rate (b_{\max}) is 0.39 assuming mature females give birth to a surviving calf every third year, and every second year if they lose their calf [$b_{\max} = 1/(3 p_0 + (1 - p_0)2) = 0.39$].

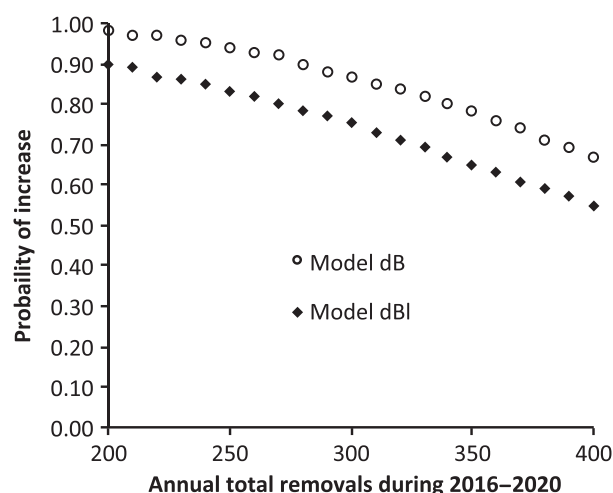


Figure 6 The probabilities of an increasing population for the two models (*dB* and *dBI*), given annual total removals between 200 and 400 individuals in the period 2016–2020.

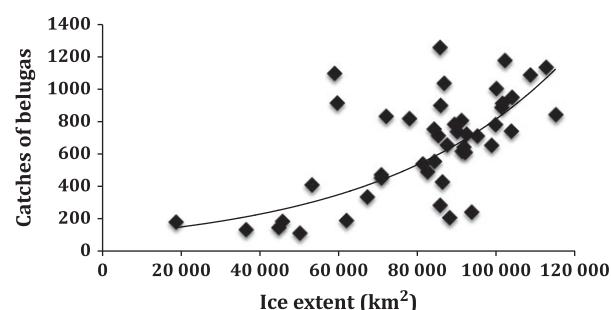


Figure 7 The relation between catches of belugas and mid-winter sea ice extent in West Greenland 1967–2012. Sea ice data are from the 'medium area' of West Greenland in Stern & Heide-Jørgensen (2003) and were updated through 2012. Catch data are from the medium option without ice entrapments updated through 2012 (see Supporting Information).

The updating of the *msyr* differs slightly between the two models: there is basically no updating in the high survival model (*dB*, Supporting Information Fig. S12), while the posterior estimate is slightly larger than the prior in the low survival model (*dBI*, Supporting Information Fig. S13). This shows that there is some trend information in the data, and that it is especially the high survival model that is in good agreement with the data. The estimated growth with a *msyr* of 3% (90% CI: 2, 5) for *dB*, and 3% (90% CI: 1, 5) for *dBI*, is slightly lower than an estimated growth rate of 4.8% (95% CI: 2.1, 7.5) for belugas in Bristol Bay, Alaska (Lowry *et al.*, 2008). Based on the more conservative model (*dBI*) with lower survival rate, and assuming that the goal is to maintain a 75% probability of increased abundance by 2020, it is estimated that the removals should be no higher than 300 belugas (see Fig. 6).

Conclusion

Based on the time series of surveys, a decline in beluga abundance in West Greenland could be detected (Heide-Jørgensen & Reeves, 1996; Heide-Jørgensen & Acquarone, 2002), and this was the main basis for the catch limit of 310 implemented on 1 July 2004 (Butterworth *et al.*, 2002; Alvarez-Flores & Heide-Jørgensen, 2004). The catch limits led to a decline in catches, but the simultaneous decline in extent of sea ice coverage off West Greenland also made it more difficult for the hunters to catch the whales as they tended to stay farther offshore and close to the ice edge (Heide-Jørgensen *et al.*, 2010). The catch reduction evidently had the intended effect on the population, which now seems to be recovering although it is still depleted (i.e. below *msyl*). Maintenance of catches at the levels proposed here should ensure continued recovery of the stock. It can therefore be concluded that the advice on sustainable harvest levels provided by NAMMCO and the implementation of catch limits in communities that were unfamiliar with restrictions on beluga hunting have enabled the stock to rebuild.

Acknowledgments

Rasmus Due Nielsen kindly provided his expertise as an observer for the aerial surveys and Norlandair provided Twin Otters and very skilled pilots for the survey. This study was funded by the Greenland Bureau of Minerals and Petroleum, the Danish Cooperation of the Environment in the Arctic (DANCEA, Danish Ministry of the Environment) and the Greenland Institute of Natural Resources. The is part of the Baffin Bay Environmental Study Program 2011–2014 conducted by the Danish Centre for Environment and Energy, Aarhus University (DCE) and the Greenland Institute of Natural Resources (GINR) for the Bureau of Minerals and Petroleum, Greenland Government, and financed by license holders in the area.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Perpendicular and forward distance distributions of beluga detections.

Figure S2. Locations of beluga sightings that have forward distances.

Figure S3. Model belEP2x.bfy perpendicular distance (left) and forward distance (right) histograms with mean detection functions in each dimension shown by the black curve

Figure S4. Q-Q plots of Model belEP2x.bfy fits in perpendicular distance (left) and forward distance (right) dimensions.

Figure S5. Model belEP2x.waitx perpendicular distance (left) and forward distance (right) histograms with mean detection functions in each dimension shown by the black curve.

Figure S6. Q-Q plots of Model belEP2x.waitx fits in perpendicular distance (left) and forward distance (right) dimensions.

Figure S7. Model belEP2x.null perpendicular distance (left) and forward distance (right) histograms with mean detection functions in each dimension shown by the black curve.

Figure S8. Q-Q plots of Model belEP2x.null fits in perpendicular distance (left) and forward distance (right) dimensions.

Figure S9. Locations of beluga sightings that have forward distances and ice cover data.

Figure S10. Perpendicular distance distribution of beluga sightings (left) and after left and right truncation (right plot; rescaled so that what was 100 m is now 0 m).

Figure S11. Half-normal detection function fit to perpendicular distance data from conventional distance sampling analysis.

Figure S12. Realized prior (curve) and posterior (bars) distributions for model *dB*.

Figure S13. Realized prior (curve) and posterior (bars) distributions for model *dB1*.

Table S1. Low and high catch history.

Table S2. Abundance estimates with cv's in parenthesis.

Table S3. Δ AIC and Cramer–von Mises goodness-of-fit statistics for fits to beluga data with *ice* variable in *x* and *y* dimensions.

Table S4. Model belEP2x.bfy stratified estimates of abundance and related parameters.

Table S5. Model belEP2x.waitx stratified estimates of abundance and related parameters.

Table S6. Model belEP2x.null stratified estimates of abundance and related parameters.

Table S7. Summary of models fitted by *hidden Markov line transect model (hmltm)*.

Table S8. Model belEP2x.null stratified estimates of abundance and related parameters with availability model 2.

Table S9. Model belEP2x.null stratified estimates of abundance and related parameters with availability model 3.